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Siamcyclops isanus sp. nov. (Copepoda, Cyclopoida, Cyclopidae), a new cave-dwelling species from northeastern Thailand

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Abstract

Siamcyclops isanus **sp. nov.** has been found from a cave in northeastern Thailand. It differs from the other member of its genus by having: 1) smooth free margin of anal operculum, 2) a different armature on the second endopod of the first and fourth legs, 3) the armature of the second endopod of the male third leg, and 4) the shape of spermatophore. The discovery of the second species from the genus *Siamcyclops* thus leads to the proposal for the generic diagnosis. The morphological differences between the genus *Siamcyclops* and other closely related genera is added.

Keywords

Groundwater, Indo-Burma region, limestone cave, taxonomy, unsaturated zone

Introduction

Thailand is a part of the Indo-Burma region, a hotspot for biodiversity in Asia (Myers et al. 2000). The country has about 6,000 caves and about 90% of those are in limestone (Dunkley et al. 2017; Jantarit and Ellis 2023). The limestone caves of northeastern Thailand are primarily located in Loei, Chaiyaphum and Nong Bua Lam Phu

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provinces (all are located in the North Phetchabun mountain range) (Choenkwan et al. 2014). Thirty-six species of cave fauna have been described from Loei Province: dipterans (1 species), diplopods (2 species: *Glyphiulus mongkon* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011 is known only from its type locality), copepods (5 species), reptiles (3 species: *Cyrtodactylus kunyai* Pauwels, Sumontha, Keeratikiat & Phanamphon, 2014 is known only from its type locality), and mammals (25 species) (Watiroyram 2021a; Jantarit and Ellis 2023). While copepod sampling in Loei Province was carried out, *Bryocyclops maholarnensis* Watiroyram, Brancelj & Sanoamuang, 2015 was found from Maholarn cave; it was the first stygobiont found in northeastern Thailand (Watiroyram et al. 2015). At present, there are 14 stygobiotic and stygophylic copepods recorded from caves in northeastern Thailand including two calanoids, three cyclopoids and nine harpacticoids (Watiroyram 2021a; Boonyanusith et al. 2024).

The genus *Siamcyclops* Boonyanusith, Sanoamuang & Brancelj, 2018, a monospecific genus, was described from Ratchaburi and Prachuap Khiri Khan provinces and its distribution appears to be restricted to the central part of Thailand (Boonyanusith et al. 2018; the present study). Among the most similar genera, *Siamcyclops* more closely resembles *Palaeocyclops* Monchenko, 1972, *Thalamocyclops* Fiers & Van Damme, 2017, and *Bryocyclops* Kiefer, 1927. The unknown species, collected along with *B. maholarnensis* from the Maholarn cave in Loei province, is proposed as a new species of the genus *Siamcyclops*.

Materials and methods

Study area

The Maholarn cave is located in Nonghin subdistrict, Nonghin district, Loei province, northeastern Thailand (Fig. 1A, B). The cave is situated in the local temple, one of the famous limestone caves visited by tourists and assumed to be at least 265 million years old (Fontaine et al. 2005). It is about 220 m long, 3–4 m wide and 6–7 m high, with a single passage. Near the entrance, there is a small pool on the rock filled by dripping water from a stalactite, which always dries out during the dry season (March – early May). During the rainy season, the rimstone pool at the end part of the cave receives a heavy flow of water dripping from the stalactites. In addition, a small opening in the cave roof allows water to flow in from outside. The cave is flooded from the far end up to the middle of its length, and mud is always found on the floor throughout the passage.

Sampling and taxonomic study

The samples were collected from a small pool near the entrance and a large rimstone pool in the innermost part of the cave (Fig. 1C, D) using a bottle with mesh size 60 μm and was fixed immediately in 70% ethanol (Brancelj 2004). Adult males and females

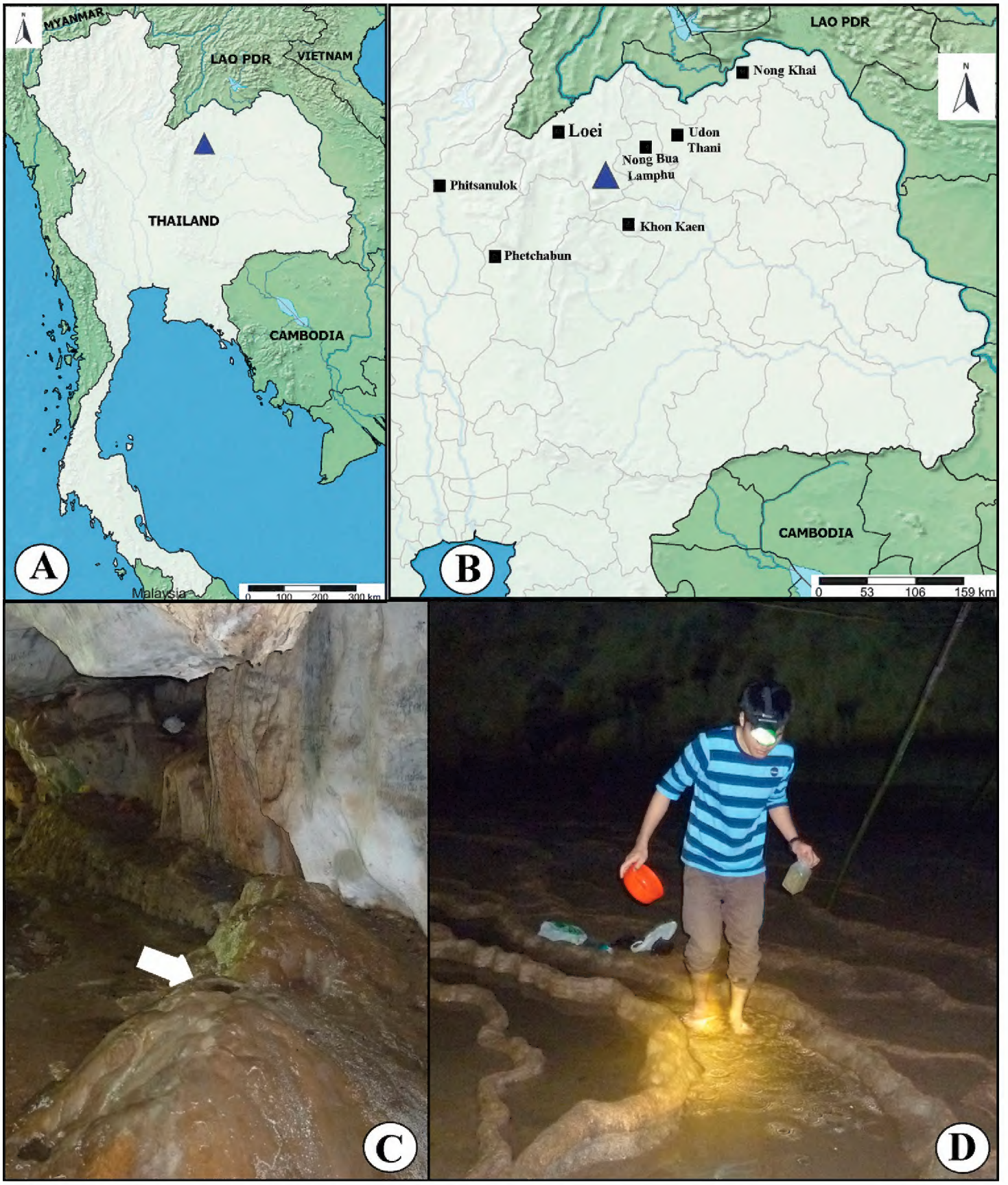

Figure 1. Map of the sampling site of *Siamcyclops isanus* sp. nov. **A** map of Thailand [triangle = location of the Moholarn Cave] **B** location of Loei Province [triangle = location of the Moholarn Cave; square = capital city nearby] **C, D** photo of the sampling site [white arrow indicates small pool at the entrance].

of copepods were sorted and preserved in 70% ethanol. Specimens were dissected under an Olympus SZ51 stereomicroscope in a mixture of glycerol and 70% ethanol (ratio ~ 1:10 v/v). Dissected specimens were mounted in pure glycerol on slides sealed with transparent nail polish and examined using an Olympus compound microscope (CX31) at 1,000 × magnification. Body length of specimens was measured using Zeiss

compound microscopy software (Axio Imager 2). The pencil drawings were made using a drawing tube (Olympus U-Da) mounted on the compound microscope. The final drawings were made using CORELDRAW® X7 graphic software (https://www.coreldraw.com/en/). Specimens for scanning electron microscopy (SEM) were dehydrated through a series of ethanol concentrations (50%, 70%, 80%, 90%, 95%, 100%, and 100% abs.) for 15 min at each concentration. Specimens were dried in a critical point dryer and mounted on stubs. Mounted specimens were coated with gold in a sputter-coater. SEM photographs were carried out using a LEO 1450VP scanning electron microscope.

Type specimens were deposited at the Thailand Natural History Museum in Pathum Thani, Thailand (THNHM) and at the Faculty of Science in Nakhon Phanom University, Thailand (NPU).

The morphological terminology follows Huys and Boxshall (1991). The abbreviations used in the text and figures are: **A** = aesthetasc; **S** = spine; **Enp** = endopod; **Exp** = exopod; **Exp-n** or **Enp-n** = exopodal segment n or endopodal segment n; **P1–P6** = swimming legs 1–6.

Results

Taxonomic section

Order Cyclopoida Burmeister, 1834
Family Cyclopidae Rafinesque, 1815

Genus *Siamcyclops* Boonyanusith, Sanoamuang & Brancelj, 2018

Type species. *Siamcyclops cavernicolus* Boonyanusith, Sanoamuang & Brancelj, 2018

Other species. *Siamcyclops isanus* sp. nov.

Emended diagnosis of the genus. Body cyclopiform, small size, with the greatest width at the cephalothorax. Pseudosegment present anterior to the genital double somite. Genital double-somite enlarged laterally, shorter than wide. Genital pore located near middle of somite length. Seminal receptacle small; anterior expansion longer and wider than posterior part. Anal operculum well developed or not, with a smooth or serrated distal margin. Antennule 11-segmented in female, 15-segmented in male. Antenna without Exp. Mandibular palp reduced, represented by three setae. P1–P3 coxa with inner seta but absent on P4. P1–P4 intercoxal sclerite with round prominences. P1 basis with inner seta. P1–P4 with 2-segmented Exp and Enp, subequal in size; setal and spines formula of Exp-2 as 5.5.5.4–5 and 3.3.3.2, respectively. P5 fused to pediger 5, with lateral seta and two ventral setae on small lobe. P6 of female with slender seta and two spiniform setae, located dorso-laterally on the simple plate of the genital double-somite; three slender setae in male. P3 Enp-2 of male with a transformed apical spine and inner subterminal seta.

***Siamcyclops isanus* sp. nov.**
https://zoobank.org/7B285B72-0665-4AE7-8F0F-0F40F5452BDB
Figs 2–6

Type locality. The Maholarn cave, Nonghin Subdistrict, Nonghin District, Loei Province, northeastern Thailand: 17°06'23.04"N, 101°52'48.54"E, 315 m altitude. Sample collected from a rimstone pool in the innermost zone, filled with dripping water.

Etymology. *Siamcyclops isanus* sp. nov. is named after 'Isan', the local name for northeastern Thailand. The species epithet is a masculine, singular adjective.

Type specimens. ***Holotype*** • one adult female dissected and mounted on one slide, THNHM-IV-20465. ***Allotype*** • one adult male dissected and mounted on one slide, THNHM-IV-20466. ***Paratypes*** • one adult female and male dissected and mounted on two separate slides, (NPU 2024-01–02) • four adult females and nine adult males stored in a 1.5 ml microtube with 70% ethanol, (NPU 2024-01–02) • one adult female and male dissected and mounted on two separate slides, NPU 2020-003 • one adult male dissected and mounted on one slide, THNHM-IV-20467. All samples were collected by the first author on 5 July 2013.

Description of adult female (holotype). Habitus (Fig. 2A) cyclopiform. Body length, excluding caudal setae, 550 μm, with prosome/urosome ratio of 1.5. Body surface ornamented with refractile points (not figured). Nauplius eye indiscernible. Posterior margin of prosomites with smooth free margin of hyaline fringe. Cephalosome completely fused with first thoracic somite, forming cephalothorax. Urosome length 212 μm; length/width ratio of 1.1. Pseudosegment present between pediger 5 and genital double-somite. Genital double-somite (Fig. 2B–D) enlarged; anterior part slightly wider than posterior part; 1.2 times as wide as long; with pair of sclerotised semi-rounded structures laterally and P6 dorsolaterally; posterior margin with irregularly serrated free hyaline fringe. Urosomites 3–4 (Fig. 2B–D) with about 1.6 times as long as wide; posterior margin with irregularly serrated free hyaline fringe. Anal somite (Fig. 2A–D) short, 1.6 times as long as wide; with a pair of dorsal sensilla at base of anal operculum. Anal operculum (Fig. 2B, D) reaching slightly beyond distal end of anal somite; semicircular; free margin smooth. Caudal rami slightly divergent (Fig. 2A–C). Caudal ramus rectangular, about 2.5 times as long as wide, without dorsal longitudinal keel. Anterolateral accessory seta (I) reduced. Lateral seta (II) pinnate, slightly shorter than 1/2 length of caudal ramus, inserted at 1/3 length of caudal ramus. Posterolateral seta (III) pinnate, strong, spine like, shorter than caudal ramus, with spinules at insertion point on ventrolateral side. Outer terminal seta (IV) pinnate, about 2.5 times as long as caudal ramus, without fracture plane. Inner terminal seta (V) pinnate, about 4.0 times as long as caudal ramus, without fracture plane. Innermost terminal seta (VI) bare; shortest. Dorsal seta (VII) pinnate, articulated, longer than caudal ramus.

Antennule (Fig. 3A). 11-segmented, not reaching posterior margin of cephalothorax. Armature formula as follows: 7.2.5.2.0+S.2.3.2+A.2.2+A.7+A. Aesthetascs cylindrical.

Antenna (Fig. 3B). 4-segmented; coxobasis smooth, with seta on distal inner corner. Enp 1–3 with small spinular rows on outer margin, Enp-1 with seta on distomedial margin; Enp-2 with medial seta and four distal outer setae; Enp-3 with seven apical setae, two of them geniculated. All setae smooth.

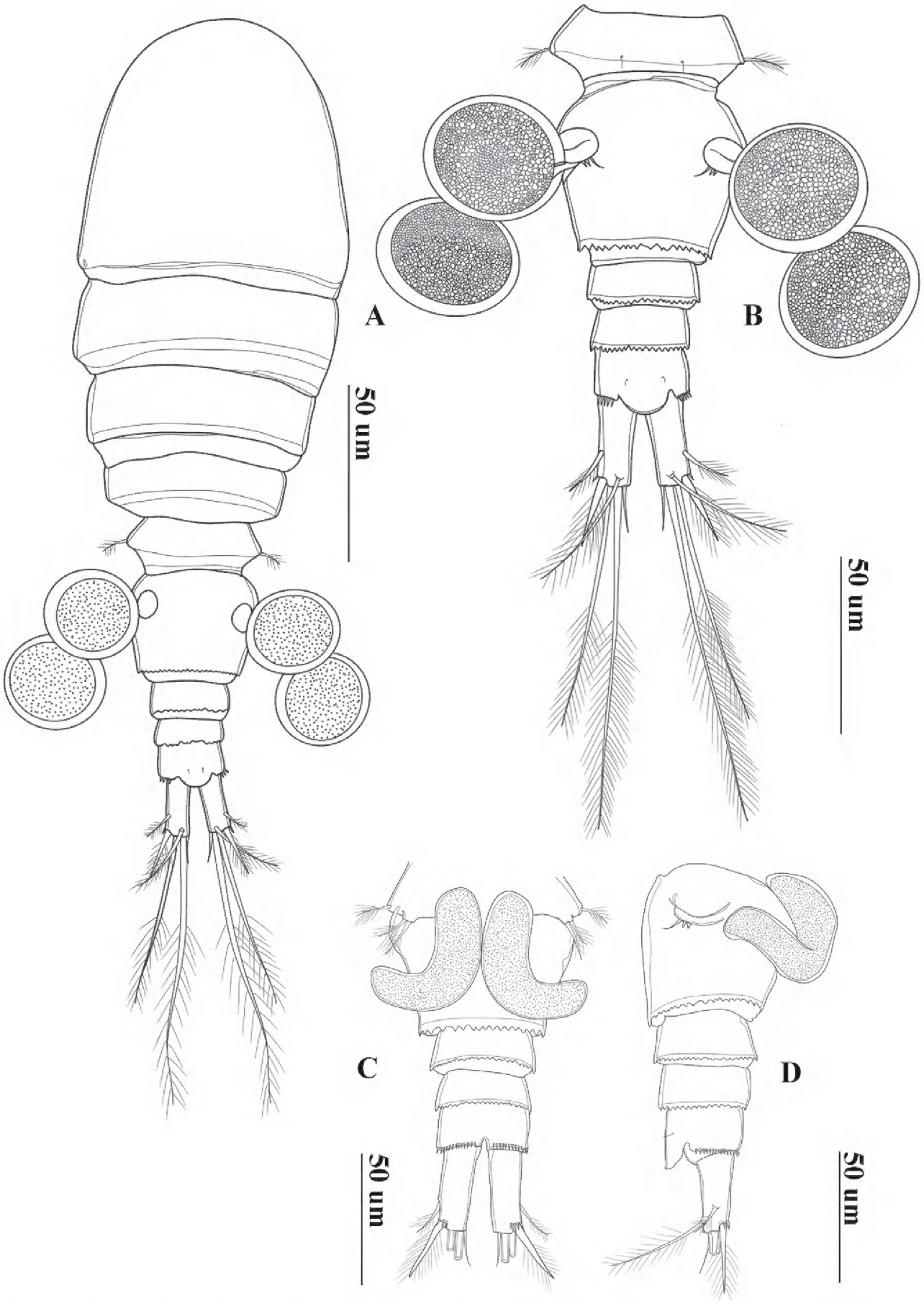

Figure 2. *Siamcyclops isanus* sp. nov., holotype female (**A, B**) and paratype female (**C, D**) **A** habitus, dorsal view **B** urosome with a pair of egg sacs, dorsal view **C** urosome with spermatophore, ventral view **C** urosome with spermatophore, lateral view.

Mandible (Fig. 3C). Gnathobase with eight strongly chitinized teeth, and a small seta dorsally. Basis very reduced, with two long bipinnate setae and a short smooth seta, representing Exp and Enp.

Maxillule (Fig. 3D). Precoxal arthrite with strongly chitinized teeth, one tricuspidate and two bicuspidate; four strong smooth setae and one spinulate seta on inner

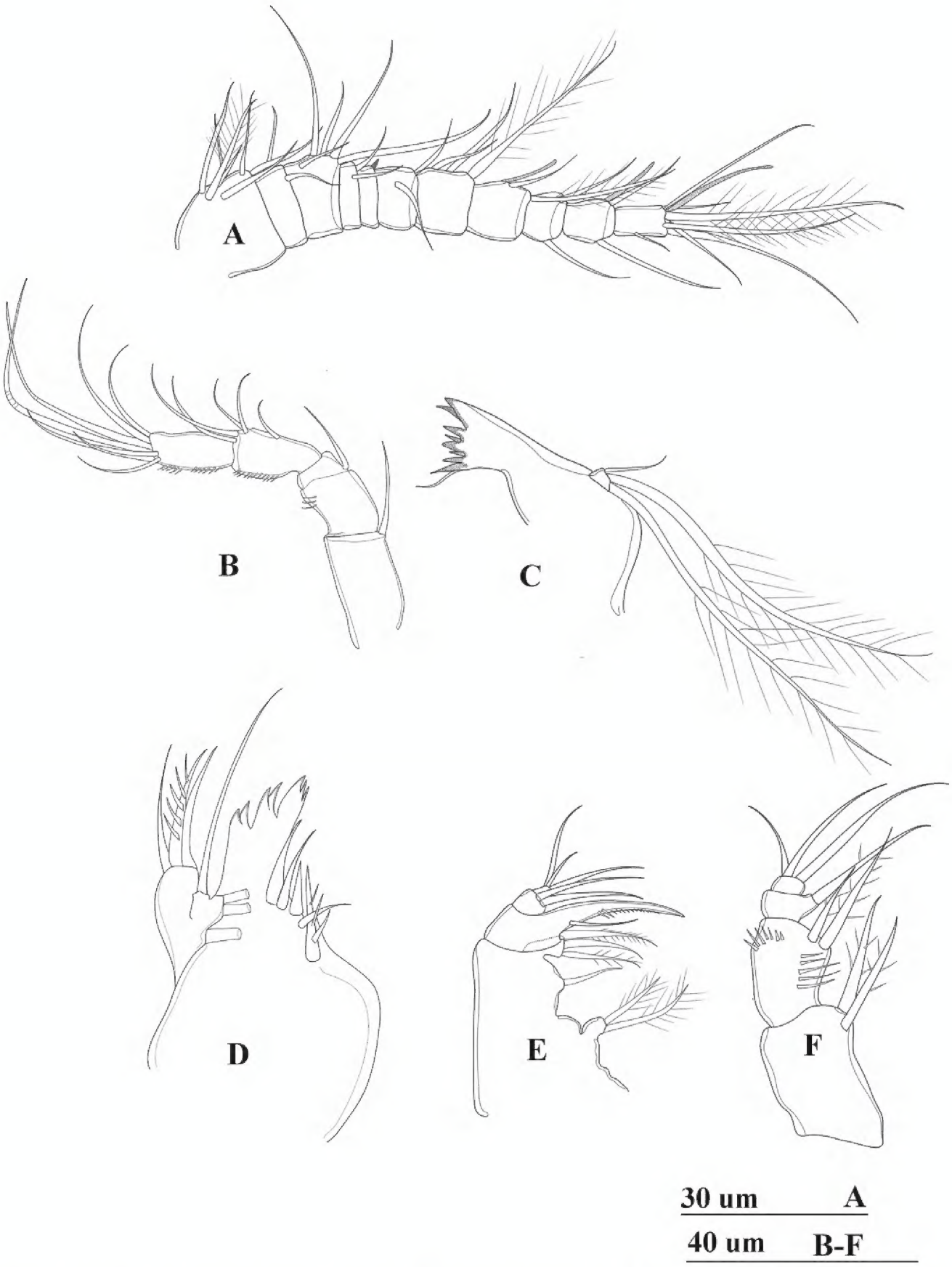

Figure 3. *Siamcyclops isanus* sp. nov., holotype female **A** antennule **B** antenna **C** mandible **D** maxillule **E** maxilla **F** maxilliped.

margin. Coxobasis with spinulate seta and two smooth setae distally. Exp completely reduced, represented by a smooth seta. Enp with three smooth setae.

Maxilla (Fig. 3E). Precoxal endite with two pinnate setae. Coxa with two endites: proximal endite with smooth seta; distal endite with smooth seta and pinnate seta. Basis drawn out into claw-like expansions, with slender seta on proximal inner margin. Two-segmented Enp: Enp-1 with two smooth setae; Enp-2 with three smooth setae.

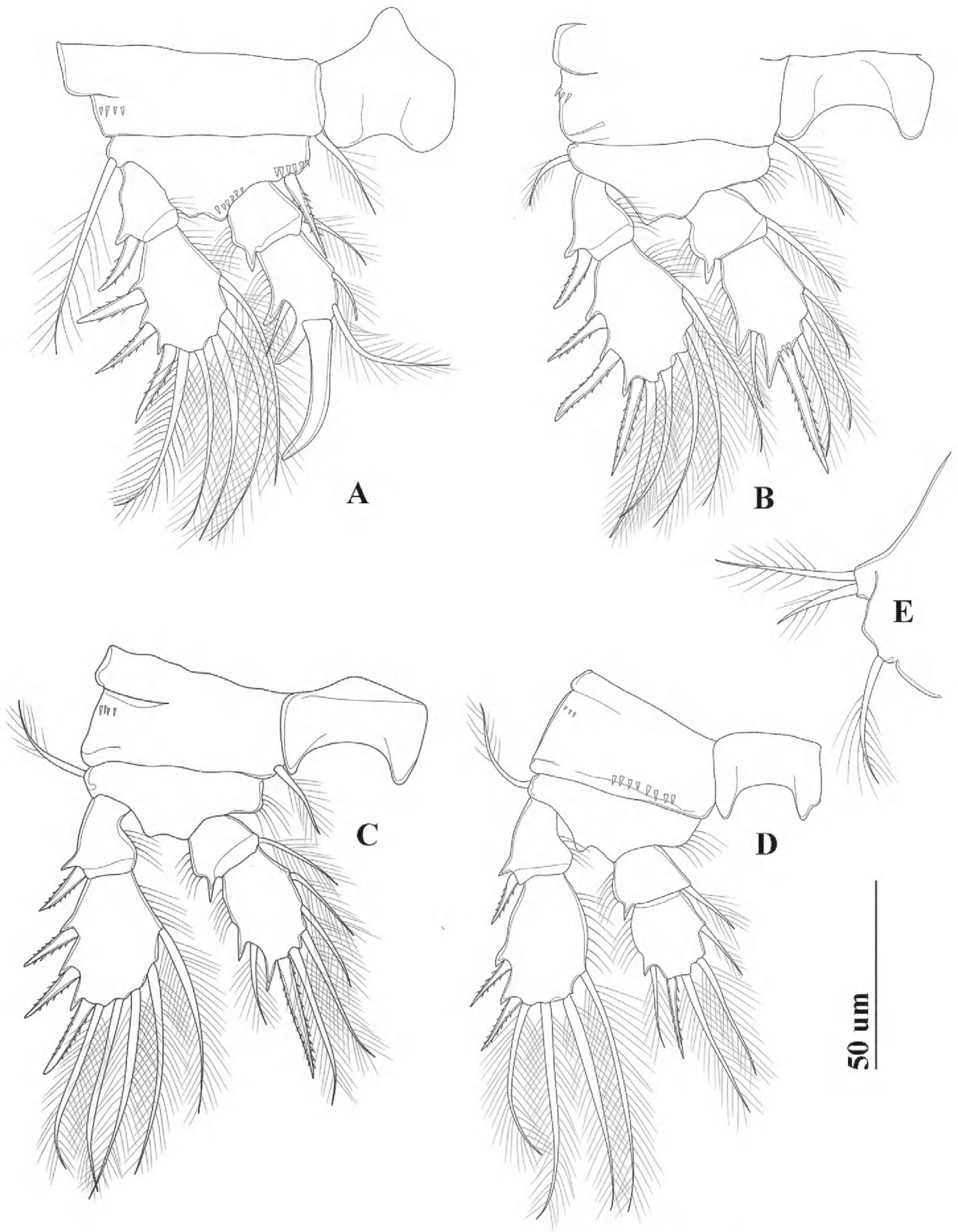

Figure 4. *Siamcyclops isanus* sp. nov., holotype female **A** P1 **B** P2 **C** P3 **D** P4 **E** P5.

Maxilliped (Fig. 3F). Syncoxa with two spinulate setae on distal inner margin. Basis with two spinulate setae on distal inner margin, accompanied by two spinule rows on its surface. Enp-1 with inner seta; Enp-2 with three apical setae; all setae smooth.

P1–P4 (Fig. 4A–D). P1–P4 with 2-segmented Exp and Enp. Exp and Enp ornamented with setules on its inner and outer margin, respectively. No blunt seta on Exp-2, all setae being equal. Armature formula (setae in Arabic numerals and spines in Roman numerals from outer-inner or outer-apical-inner margins) as follows:

	Coxa	Basis	Exp	Enp
P1	0-1	1-I	I-0; III-2-3	0-1; 1-I-2
P2	0-1	1-0	I-0; III-2-3	0-1; 1-I+1-2
P3	0-1	1-0	I-0; III-2-3	0-1; 1-I+1-3
P4	0-0	1-0	I-0; II-2-2	0-1; 0-I+1-2

P1 (Fig. 4A). Basis with small spinules near its insertion. Exp slightly larger than Enp. Exp-1 much smaller than Exp-2. Exp-2 about twice as long as wide. Enp-2 larger than Enp-1, about 2.0 times. Enp-2 with robust apical seta, as long as Enp-1 and Enp-2 combined, its tip bent outward; distal inner seta as long as apical spine, the two remaining setae shorter.

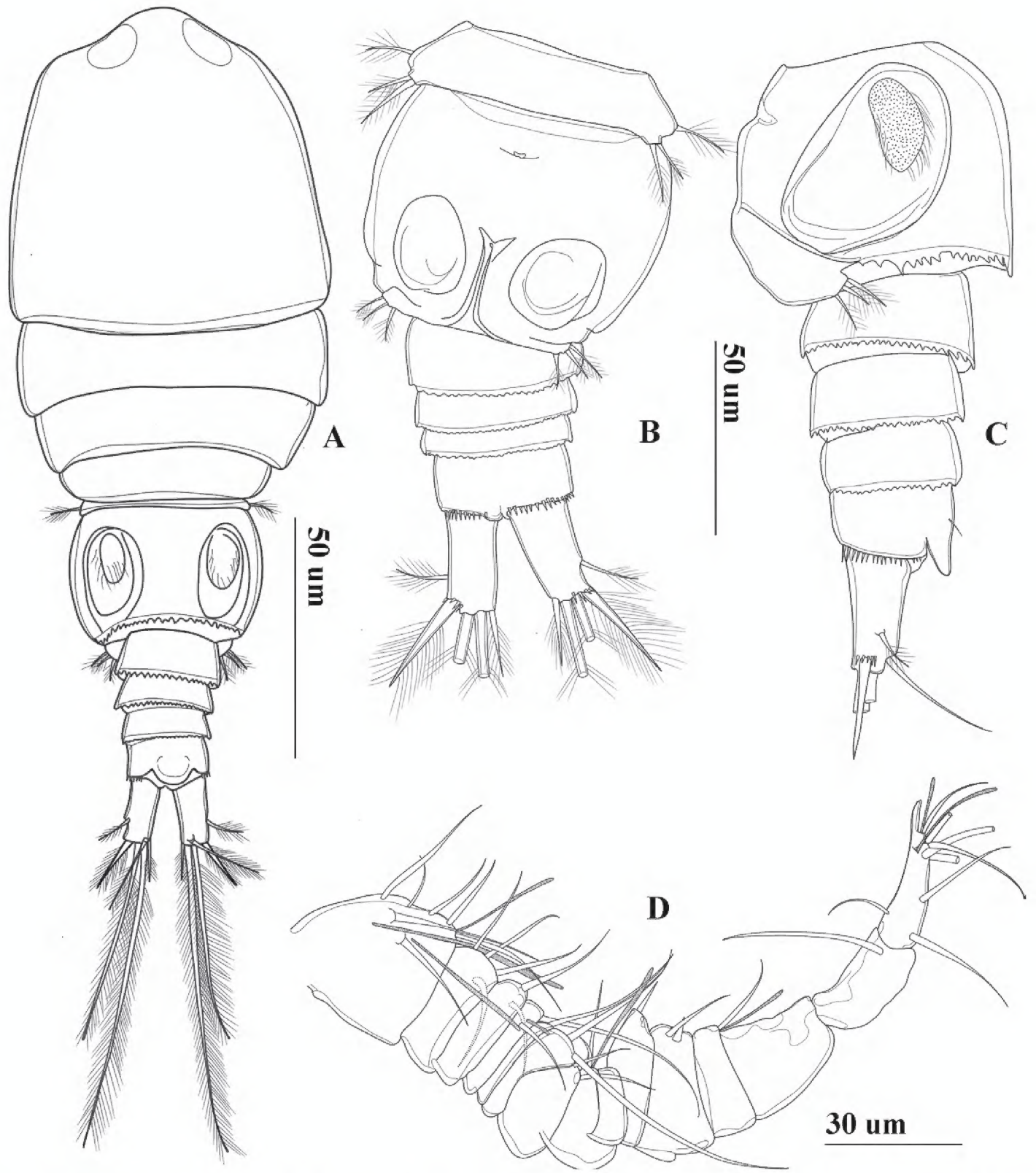

Figure 5. *Siamcyclops isanus* sp. nov., allotype male **A** habitus, dorsal view **B** urosome, ventral view **C** urosome with urosomite 1, lateral view **D** antennule.

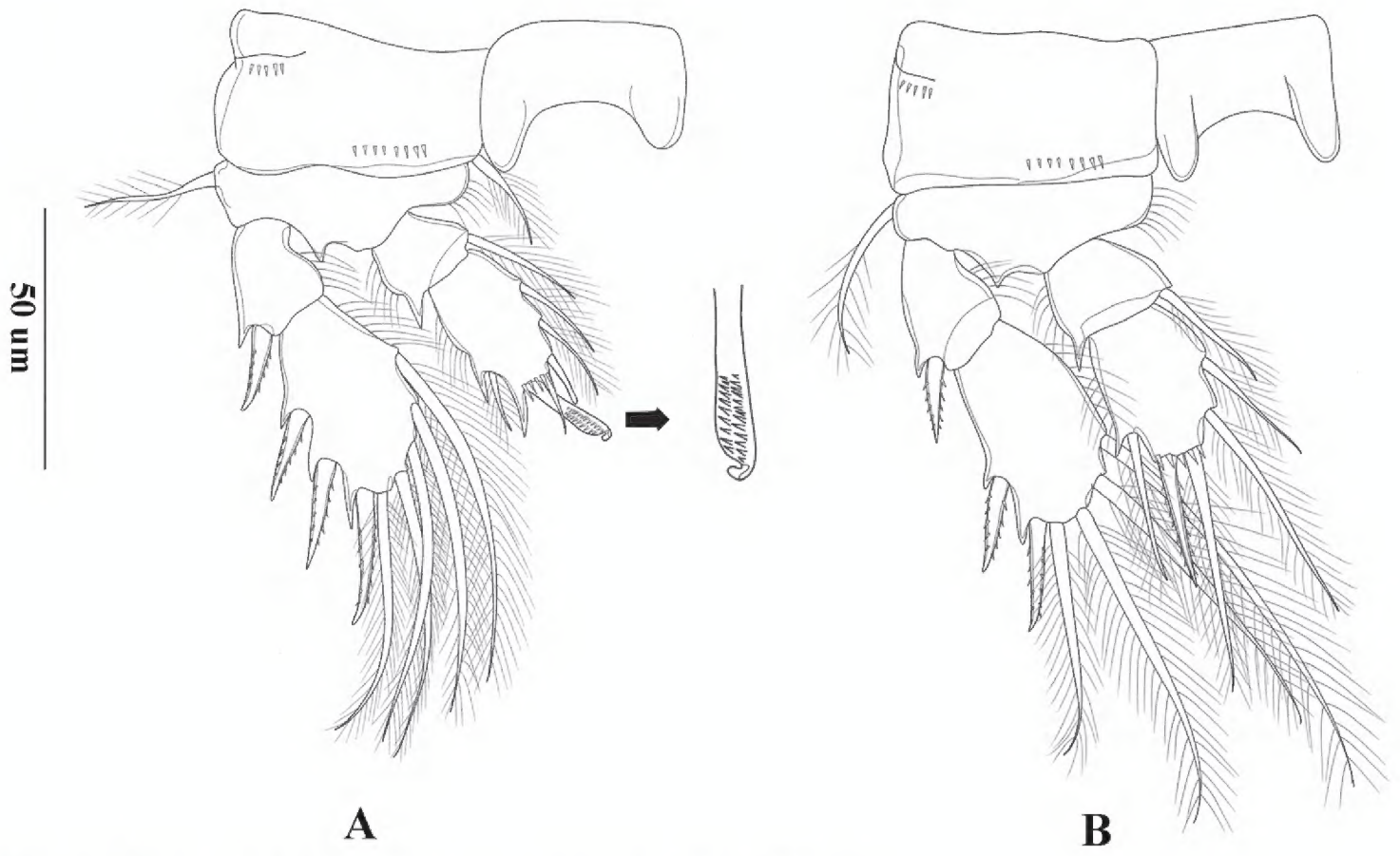

Figure 6. *Siamcyclops isanus* sp. nov., allotype male **A** P3 **B** P4.

P2 (Fig. 4B). Similar to P1 but lateral seta of basis shorter. Enp-2 with strong spinulated apical spine, with strengthened tip; two setae as long as apical spine but two remaining setae shorter.

P3 (Fig. 4C). Similar to P2 but lateral seta on basis longer, Enp-2 with slightly less robust apical spine. Enp-2 with two setae longer than apical spine, three remaining setae shorter.

P4 (Fig. 4D). Exp-1 and Exp-2 with weakly spinulated outer spines. Exp-2 twice as long as wide; three inner setae longer than Exp-1 and 2 combined, outermost seta shortest. Enp-1 slightly shorter than wide, Enp-2 about 1.3 times as long as wide. Enp-2 with slender apical spine, short as long as segment bearing it; outer and innermost seta shorter than apical spine, two remaining setae longer than apical spine.

P5 (Fig. 4E). Completely fused to pediger 5, proximal segment represented by lateral seta, and distal segment retains two pinnate apical setae on a small lobe. Lateral seta slightly longer than apical inner seta; apical inner seta about 1.3 times as long as apical outer one.

P6 (Fig. 2D). Reduced to a semi-circular plate, with three short elements: dorsal seta thin and short, two ventrally positioned elements spiniform.

Egg sac (Fig. 3A, B). Each sac with two large eggs**;** each egg about 70 μm in diameter**.**

Spermatophore (Fig. 3C, D). Three-dimensional C-shaped.

Description of adult male (allotype). Body length (Fig. 5A), excluding caudal rami, 540 μm; smaller than female. General segmentation and ornamentation (Fig. 5A–C) similar to female except genital somite and antennules. Genital somite (Fig. 5B, C) not fused with urosomite 3 like in female, enlarged laterally; 1.3 times as wide as long; with pair of sclerotised rounded structures dorso-laterally; posterior

margin with irregularly serrated free hyaline fringe. Urosomites 3–5 (Fig. 5A–C) with about 1.5 times as long as wide; posterior margin with irregularly serrated free hyaline fringe.

Antennule (Fig. 5D). 15-segmented, geniculate. Armature formula as follows: 6+3A.4.2. 2+A.1.2.2.2+A.0.1.1+S.1+A.0.1.8+2A.

Antenna, mouthparts, P1, P2 and P5 similar to female.

P3 (Fig. 6A). Exp similar to female. Enp-2 shorter than wide, Enp-2 about 1.5 times as long as wide. Enp-2 with transformed spine and smooth seta apically: transformed spine bent inward, with round tip bent outward, serrated by two rows of spinules on distal half of it. Inner subterminal seta transformed to spine-like seta, strong, bare, with blunt tip.

P4 (Fig. 6B). Exp and Enp similar to female but Enp with slightly longer, about 1.5 times as long as wide.

P6 (Fig. 5B, C). Reduced to simple plate, represented by three subequal pinnate setae.

Variability. One of female (out of five) has P6 with two elements.

Distribution. Known only from the type locality.

Differential diagnosis. The new species is similar to *S. cavernicolus* Boonyanusith, Sanoamuang & Brnacelj, 2018 in the following characteristics: 1) mandibular palp with three setae; 2) Exp and Enp of P1–P4 are subequal; 3) spine formula of P1–P4 Exp-2 is 3.3.3.2; 4) P4 lacks coxal seta; 5) P4 intercoxal sclerite with round distal margin; 6) P5 fused to pediger 5, remaining small unsegmented lobe; 7) P6 with three elements (see Table 1). However, the new species differs from *S. cavernicolus* in: 1) anal operculum smooth and unproduced over segment bearing it (serrated free margin and well-developed in *S. cavernicolus*); 2) P1 Enp-2 with four elements (five elements in *S. cavernicolus*); 3) P3 Enp-2 with six elements in male (five elements in *S. cavernicolus*); 4) P4 Exp-2 with four setae (five setae in *S. cavernicolus*); 5) spermatophore is three-dimensional C-shaped (L-shaped in *S. cavernicolus*).

Table 1. Morphological differences between the genus *Siamcyclops* and the closely related genera.

Genera characteristics	*Bryocyclops*	*Thalamocyclops*	*Palaeocyclops*	*Siamcyclops*
Both sexes				
Mandibular palp	With 1 seta	With 1 seta	Unknown	With 3 setae
Annal operculum	Well-developed	Well-developed	Well-developed	Normal – Well-developed
Size of Exp versus Enp on P1–P4	Larger	Larger	Subequal	Subequal
Spine formula of P1–P4 Exp-2	3.3.3.3(4)	3.3.3.3	2.3.3.3	3.3.3.2
Setal formula of P1–P4 Exp-2	5(4).5.5.4	5.5.5.4	5.5.5.4	5.5.5.5(4)
Coxal seta of P1–P4	1(0).0.0.0	1.0.0.0	1.1.1.0	1.1.1.0
Intercoxal sclerite of P4	Acute	Acute	Acute	Round
P5 segment	Absent –prominence (shape **a**)	Large lobe (shape **c**)	Absent (shape **a**)	Small lobe (shape **b**)
Female				
Number of segments on P4 Enp-2	1 or 2	1	2	2
Number of setae and spines on P4 Enp-2	4	4	5	5
Male				
Number of setae and spines on P6	3	3	2	3

The SEM photos of P5 show the degree of reduction in *Siamcyclops* and *Bryocyclops* species. The distal segment of P5 is reduced to a small lobe on pediger 5 in *Siamcyclops* (Fig. 7C, D), while it is more reduced in *Bryocyclops*, where it is represented by a small prominent knob (Fig. 7A, B). In addition, the setae tend to be shorter and stronger, resembling spiniform setae in some species (Fig. 7B), which is advantageous for species living in the confined spaces of the epikarst.

Key to species of the genus *Siamcyclops*

1 Anal operculum well-developed, with serrated free margin; P4 Exp-2 with five setae; the female P1 Enp-2 with five elements; the male P1 & P3 with five elements each ..... ***S. cavernicolus***

2 Anal operculum short, with smooth free margin; P4 Exp-2 with four setae; the female P1–Enp-2 with four elements; the male P1 & P3 Enp-2 with four and six elements, respectively ..... ***S. isanus* sp. nov.**

Discussion

In terms of oligomerization, many characters were used for species and generic determination which are apomorphic traits developed for living in semiterrestrial and subterranean habitats (Watiroyram 2018a, 2021b; Hołyńska et al. 2024). However, characters under strong evolutionary selection should be used with caution for taxonomic purposes because they may represent parallel evolution (and sometimes convergence). The subterranean Cyclopinae have much reduced mandibular palp, presenting a tiny distinct segment until a reduction to 1–3 setae only; small body size (usually less than 550 μm), short antennule (10 or 11 segments, usually reaching two-third of cephalothorax length), and reduced swimming legs (Fiers et al. 1996; Pesce 1996; Fiers and van Damme 2017). Pesce (1996) noted that the lineage of the *Bryocyclops* group (including *Siamcyclops*) shows the most reduced P5 form of the family Cyclopidae (the sixth morphological group sensu Pesce 1996) in having P5 completely fused to the somite, represented by a prominence of the remaining distal segment or absent; P1–P4 has 2-segmented Exp and Enp (some species have 1-segmented Exp and Enp; for example, *B. fidjiensis* with 1-segmented Exp, while *B. jayabhumi*, *B. maholarnensis*, *B. muscicola*, *B. muscicoloides*, *B. trangensis* with 1-segmented Enp in females). The setae and spines of their legs are also reduced in number, size and structure. For example, *Siamcyclops* species lack P4 coxal seta, whereas some species of *Bryocyclops* lack this seta on all P1–P4 swimming legs; setae tend to be shorter, and stronger than those from epigean habitats, or the setae are transformed to be spiniform (see fig. 4D in Watiroyram et al. 2012; Figs 6A, 7B in the present study).

The genus *Siamcyclops* has a transformed apical spine on P3 Enp-2 in the male, coxal seta on P4 and P5 segment absent in both sexes, indicating that it closely resembles the genus *Palaeocyclops* Monchenko, 1972 [*Bryocyclops* (*Palaeocyclops*) *jankowskajae* Monchenko, 1972 is an alternative name used by Walter and Boxshall (2024)],

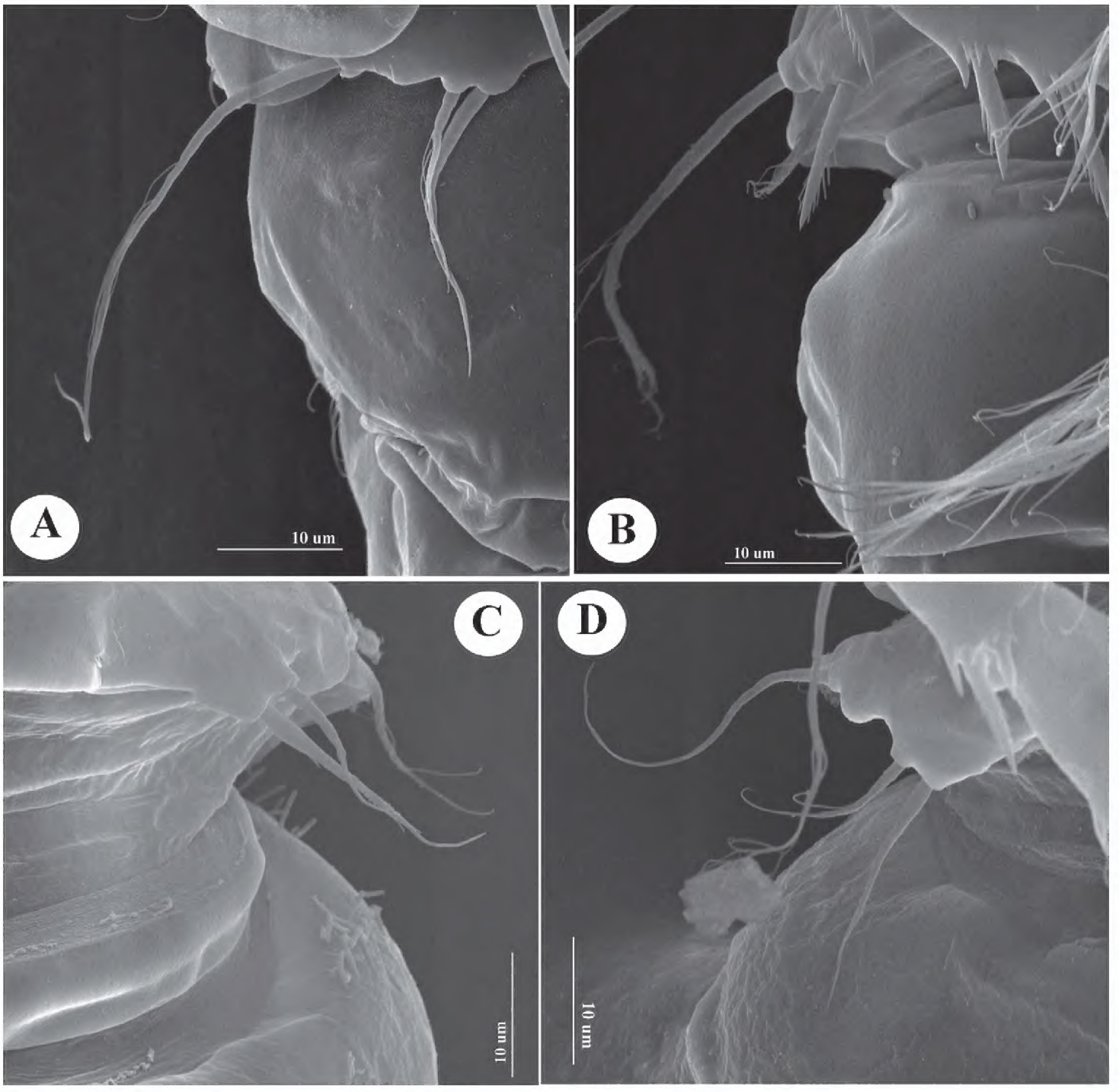

Figure 7. Photographs taken using scanning electron microscope **A** *Bryocyclops asetus* Watiroyram, 2018 **B** *B. jayabhumi* Watiroyram, 2021 **C** *Siamcyclops cavernicolus*, male **D** *S. cavernicolus*, female.

Thalamocyclops Fiers & Van Damme, 2017, and *Bryocyclops* Kiefer, 1927 (Fiers and van Damme 2017; Watiroyram 2021b). The transformed apical spine of the male P3 Enp-2 is also present in the genus *Itocyclops* Reid & Ishida, 2000 but P4 bears a coxal seta and P5 has a distinct segment in *Itocyclops*. After re-examining the P5 of *Siamcyclops* and *Bryocyclops* genera collected from Thailand, we classified the P5 of the *Bryocyclops* group sensu Pesce (1996) into three shapes based on the degree of reduction in the distal segment (absent or with a prominence/knob, small lobe, or large lobe): shape a with dorsal seta and two ventral setae (usually spiniform) fused to somite or inserted on a small prominence, versus shapes b and c with dorsal seta and two ventral setae on a lobe of an ancestral distal segment. The genus *Thalamocyclops* retains the vestigial P5 distal segment (shape c; with large lobe) more than the genus *Siamcyclops* (shape b; with small lobe; Figs 4E, 5B, 7C–D) followed by *Bryocyclops* (shape a; absent

or with small prominence; Fig. 7A, B) and *Palaeocyclops* (shape a; prominence absent). Among closely related genera, *Siamcyclops* shows the least reduced form (i.e., a plesiomorphic trait) in contrast to *Bryocyclops* s. str. such as the mandibular palp with three setae, an unproduced anal operculum and P4 intercoxal sclerite, subequal size of exopodal and endopodal segments, presence of coxal seta on P2–P3, and a number of segments and setae on P4 (see Table 1).

In the *Bryocyclops* group sensu Pesce (1996), the anal operculum is well-developed in the genus *Bryocyclops* s. str., whereas it is incompletely developed, semicircular or subquadrate and with a smooth distal free margin in the remaining genera. Both scenarios are also present in the genus *Microcyclops*, being probably due to parallel evolution or convergence, or within the genus *Siamcyclops* (*S. cavernicolus* has a well-developed anal operculum but the new species does not). Based on our knowledge of the genera *Bryocyclops* and *Siamcyclops*, the shape of the spermatophore and refractile points is varied and not specific to these genera (Watiroyram 2021b; the present study). For example, the new species has C-shaped spermatophore versus L-shaped in *S. cavernicolus*, while most species of the genus *Bryocyclops* have a pair of bean-shaped spermatophore, whereas other shapes are present in *B. asetus* Watiroyram, 2018 (inverted V-shaped) and *B. trangensis* Watiroyram, 2018 (a pair of spermatophores is arranged in a straight line). Refractile points on the body surface are also not a unique apomorphy for the genera *Bryocyclops* and *Siamcyclops*: the new species has such cuticular pits but *S. cavernicolus* has not (Watiroyram 2018a, 2018b; the present study).

Our findings indicate that the genus *Siamcyclops* is endemic to Thailand, with two species having a well separated distribution area: *S. cavernicolus* in the central part and the new species in the northeastern part of the country. Regarding copepod samples taken by the first author, *S. cavernicolus* is also distributed southwards to Prachuap Khiri Khan province (Watiroyram 2021a). They are likely epikarstic species, well-adapted to a benthic lifestyle, thriving in both the confined spaces of the epikarst and the larger pools within caves as shown by the presence of the pseudosegment anterior of the genital double-somite, like in *Bryocyclops* species (Fig. 7B, C; Watiroyram 2018a). The pseudosegment is not present in *Thalamocyclops*, conforming to its habitats, which features a large space and a water volume, suitable for good swimmers. Fiers and Van Damme (2017) collected many adults and different stages of juveniles of *Thalamocyclops pachypes* from weathered limestone crevices, indicating that they inhabit these crevices for growth and breeding. In contrast, species of *Siamcyclops* and *Bryocyclops* collected from Thailand typically have a pseudosegment for living in small spaces, as indicated by the fact that adults are usually collected rather than juveniles (i.e. they accidentally drop from the ceiling of the cave, especially in the rainy season). Observations over many years (2013–present) allowed to collect *B. moholarnensis* only in the small pool near the entrance (Fig. 1C), while *S. isanus* sp. nov. was found in a large pool at multiple points in the inner section of Maholarn Cave (Fig. 1D).

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